On Abundance, Phenology and Natural History of Symphyla from a Mixedwater Inundation Forest in Central Amazonia, Brazil

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ABSTRACT

Inundation forests in Central Amazonia are covered by several metres of floodwater for 5-7 months each year, due to the monomodal flood pulse of rivers. Terrestrial invertebrates have adapted to this ecosystem by evolving several survival strategies. The Symphyla of a mixedwater inundation forest near Manaus comprised solely terricolous species, which represented non-migrants and migrants. Migratory reaction of *Hanseniella arborea* Scheller, 1979 was vertical, with temporal ascent of adults into tree trunks. The non-migrating species *Symphylella adisi* Scheller, 1992 and *Ribautiella amazonica* Scheller, 1984 had dormant stages under water. Subadults and advanced juvenile stages of *R. amazonica* spent the inundation period in naturally available retreats (inside tree roots). During the non-inundation period, abundance of this species was highest (52.6%) when compared to *H. arborea* (39.4%) and *S. adisi* (7.9%) of the total catch (n = 2139 specimens). Vertical distribution of all species in the soil (0-14 cm depth), their life cycle and the vertical migration of *H. arborea* are discussed with respect to abiotic factors in the study area.

RÉSUMÉ

Abondance, phénologie et histoire naturelle des symphyles d'une forêt inondable en Amazonie Centrale, Brésil.

Les forêts inondables de l'Amazonie Centrale sont couvertes par plusieurs mètres d'eau durant 5 à 7 mois de l'année, à cause de la fréquence d'inondations monomodales des rivières. Les invertébrés terrestres se sont adaptés à ce type particulier d'écosystème en faisant évoluer plusieurs stratégies de survie. Les symphyles d'une forêt inondable d'eau mixte près de Manaus comportent uniquement des espèces terricoles, représentées par des formes migratrices et non-migratrices. La migration de *Hanseniella arborea* Scheller, 1979 s'effectue verticalement, avec un déplacement temporaire d'adultes sur les troncs d'arbres. Les espèces non-migratrices *Symphylella adisi* Scheller, 1992 et *Ribautiella amazonica* Scheller, 1984 présentent, sous l'eau, des états de dormance. Les subadultes et les stades juvéniles avancés de *R. amazonica* passent la période d'inondation dans des retraites naturelles accessibles, notamment le système racinaire des arbres. En dehors de la période d'inondation, l'abondance de ces espèces est plus élevée (52,6%) que celles de *H. arborea* (39,4%) et de *S. adisi* (7,9%) par rapport au total des captures (n = 2139 individus). La répartition verticale de toutes les espèces dans le sol (0-14 cm de profondeur), leur cycle de vie et la migration verticale de *H. arborea* sont discutés par rapport aux facteurs abiotiques du site d'étude.

ADIS, J., DE MORAIS, J. W. & SCHELLER, U., 1996. — On abundance, phenology and natural history of Symphyla from a mixedwater inundation forest in Central Amazonia, Brazil. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 607-616. Paris ISBN : 2-85653-502-X.

Source : MNHN, Paris

INTRODUCTION

Inundation forests in Central Amazonia and their adjacent shores are covered by several metres of floodwater for 5-7 months each year due to the monomodal periodic flood pulse of rivers (cf. JUNK *et al.*, 1989). Terrestrial invertebrates have adapted to this ecosystem by evolving several "survival strategies" (cf. ADIS, 1992a). The fauna comprises both terricolous and arboricolous animals. Both groups include non-migrants and migrants. Migratory reaction of terricolous animals is horizontal (following the high water line), vertical (temporal ascent to trunk or canopy) or includes a temporal flight to upland forests. Non-migrants have active or dormant stages under water. The latter pass inundation in naturally available retreats, in self-made retreats or as eggs. Non-migrant arboricolous animals reproduce and live exclusively in the trunk and canopy region, whereas migrants include life stages that live on the ground as well. Characteristics and examples of species for each of these categories are given by ADIS (1992a, b). In this paper, adaptive reaction of Symphyla from a mixed water inundation forest near Manaus to the annual flooding is discussed. Abundance, phenology and the natural history of three species are compared with data already known from symphylans inhabiting blackwater inundation forests in the Rio Negro valley (cf. ADIS & SCHELLER, 1984; SCHELLER & ADIS, 1984).

STUDY AREA AND METHODS

The study site was at Lago Janauarí (03°20'S, 60°17'W), situated on a spit between the Rio Negro and the Rio Solimões about 10 km from Manaus, across the river. The region was influenced by blackwater of the Rio Negro during low water-level and by whitewater of the Rio Solimões during the high water period. The study site in this seasonal mixed water inundation forest (cf. PRANCE, 1979) was flat and had no direct connection with non-flooded dryland (= upland) areas, which were several km distant (comp. Fig. 18 in IRMLER, 1975). The soil consisted of clay, predominantly montmorillonite, which represented alluvial deposits of the Rio Solimões. A scanty litter layer was formed during the non-inundation period (August/September - April/May). It was mostly carried out of the forest by the current of the annual floodwaters and/or partially covered by sediments deposited during inundation. Further information on the study site is given by ERWIN (1983), IRMLER (1975) and ADIS & RIGHI (1989).

Symphylans evaluated for this study were collected between June, 1987 and May, 1988. In 1987, inundation lasted until end of July. The study area was not flooded again until early May, 1988. On the forest floor, four ground photo-eclectors (= emergence traps) provided data on the activity density of symphylans. Ground photo-eclectors are round, tent-like capture devices which cover a basal area of 1 m^2. They consist of lateral plastic walls, a roof of black cloth, a transparent collecting box on top and a pitfall trap inside the apparatus. Trunk ascents and descents were detected at bi-weekly intervals with arboreal photo-eclectors (= funnel traps) on one tree trunk each throughout the collecting period. The traps consisted of four connected capturing funnels of black cloth, each with a transparent collecting box at the funnel mouth, and formed a closed ring around the trunk. The funnel opening faced either the forest floor (for trunk ascending animals) or the canopy (for trunk descending animals). Traps for trunk ascents were mounted on *Virola surinamensis* (ROL.) WARB. (Myristiaceae) and traps for trunk descents on *Hevea spruceana* MÜLL. ARG. (Euphorbiaceae), two dominant tree species in the study area. The killing/preserving agent used in all photo-eclectors on soil and trunk was aqueous picric acid solution (without detergent), which is known to be mostly neutral in terms of attraction or repellence in temperate zones (ADIS, 1979). In one of the four ground photo-eclectors, however, an aqueous formaldehyde solution (3%) was utilized. All capture devices are fully described by ADIS (1981) and FUNKE (1971) who also explain their mode of utilization and function. In addition, the distribution of symphylans in the soil was studied between August, 1987 and May, 1988 (non-inundation period). Once a month (cf. Figs 4, 8, 12) six soil samples were taken at random along a transect with a split corer (= steel cylinder with lateral hinges; diameter 21 cm, length 33 cm), which was driven into the soil by a mallet. Each sample of 14 cm was then divided into four subsamples of 3.5 cm each. Animals were extracted from subsamples following a modified method of KEMPSON (ADIS, 1987). In addition, symphylans were obtained from soil samples which were taken under water in August 1988 (end of flood period) as described above and subsequently extracted by means of a flotation method via sugar water (for methodology see ADIS *et al.*, 1989).

Seasonal inundation forests in Central Amazonia are subject to a rainy season (December - May: average precipitation 1550 mm), and a "dry" season (June - November: average precipitation 550 mm, but each month has some rain events; cf. RIBEIRO & ADIS, 1984). Vertical distribution of Symphyla in relation to changing conditions of soil moisture content, temperature and pH was statistically evaluated with the linear correlation test (CAVALLI-SFORZA, 1972), using the original field data. This method was also used to evaluate the activity of Symphyla on the soil surface and tree trunks in relation to insolation, precipitation, temperature and humidity of the air. The taxonomic work for this paper was done by U. SCHELLER (cf. SCHELLER, 1979, 1992; SCHELLER & ADIS, 1984), the collection and the evaluation of

Source : MNHN, Paris

field data by J. ADIS and J. W. DE MORAIS. Symphylans sampled were classified as juveniles (8, 9 and 10 pairs of legs), subadults (11 pairs of legs) and adults (12 pairs of legs). For subadults and adults sex was determined according to CHARDARD (1947) and SCHELLER (1979).

RESULTS AND DISCUSSION

A total of 2386 Symphyla were collected in the seasonal mixedwater inundation forest under study. Out of these, 97% could be classified to species and developmental stages. The majority were juveniles (48% of the total catch; n = 1105), 39% were adults (n = 899) and 13% subadults (n = 312). They comprised three species: *Ribautiella amazonica* Scheller, 1984 and *Symphylella adisi* Scheller, 1992 (Scolopendrellidae) were found solely in the soil (by soil extraction). *Hanseniella arborea* Scheller, 1979 (Scutigerellidae) was caught on the soil surface (in ground photo-eclectors) and also during trunk ascents and descents (in arboreal photo-eclectors).

During the non-inundation period, 79% of all symphylans obtained by soil extraction from the 0-14 cm cores were caught in the top 7 cm, irrespective of their developmental stage (cf. Fig. 1). Abundance of *R. amazonica* was highest (53%; 542 ind. m-2 month-1), when compared to *H. arborea* (39%: 406 ind. m-2 month-1) and *S. adisi* (8% of the total catch; 82 ind. m-2 month-1). The highest population density, of 1853 ind. m-2, was recorded during the dry season (in October, 1987) and the lowest, of 260 ind. m-2, at the beginning of the non-inundation period (in August, 1987). Average abundance of Symphyla in the soil of the seasonal mixedwater forest (1766 ind. m-2 month-1) was about nine times higher than the average from a seasonal blackwater inundation forest (208 ind. m-2 month-1; ADIS & SCHELLER, 1984; SCHELLER & ADIS, 1984).

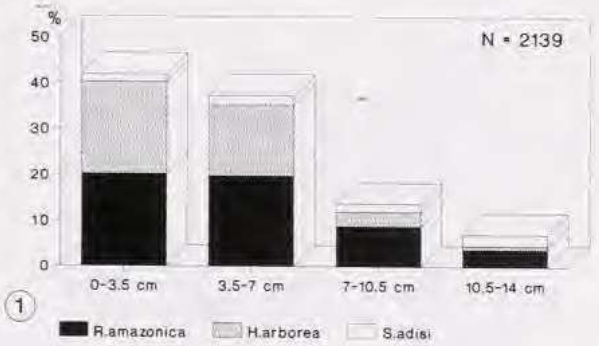

FIG. 1. — Distribution of Symphyla species in the soil. Monthly samples taken every 3.5 cm to a depth of 14 cm between August, 1987 and April, 1988 (non-inundation period) in a seasonal mixedwater inundation forest at Lago Janauarí; total catch = 100%.

Data from this study provided conclusive information on the life cycle, habitat and ecology of the three Symphyla species found.

Ribautiella amazonica Scheller (Scolopendrellidae)

This terricolous non-migrating and univoltine species reaches 2.1 mm in length. It is known to pass inundation in the soil of seasonal blackwater inundation forests inside tree roots in a dormant state (ADIS, 1992b). This behaviour was reconfirmed for *R. amazonica* from the seasonal mixedwater forest, where subadults and the last juvenile stage (10 pairs of legs) were obtained by flotation of soil samples which were taken under water during forest inundation. Shortly after the floodwater had receded from the forest (in 1987 at the end of July), these symphylans had moulted to subadults and adults (Fig. 4).

Soil extraction data, indicated that reproduction took place in the early part of the non-inundation period, as first juveniles of the offspring occurred from September onwards, four weeks after the forest floor had dried. *R. amazonica* is considered hemiedaphic, as 76% of all specimens extracted from soil samples in 1987/88 were found in the top 7 cm, irrespective of their developmental stage (Fig. 2). This is in contrast to data obtained from the seasonal

Source : MNHN, Paris

blackwater forest, where the species was considered euedaphic, as 86% of all specimens occurred below 7 cm soil depth (ADIS, 1992b).

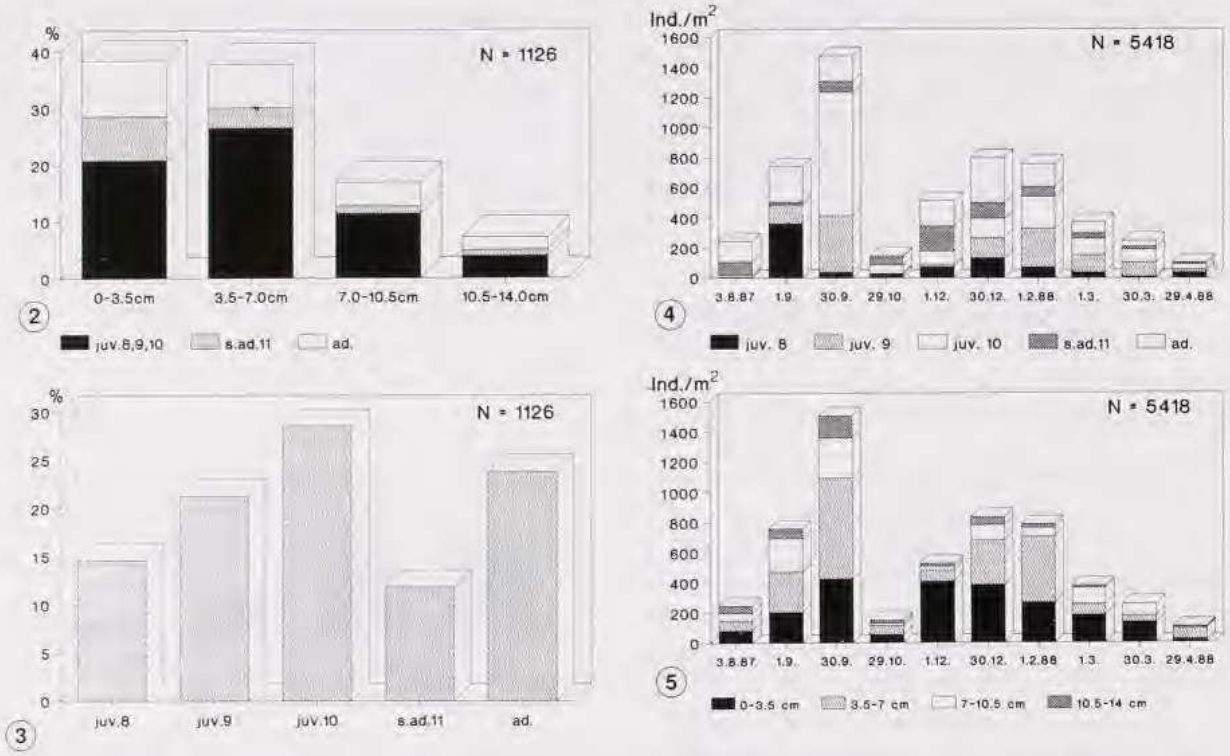

FIG. 2. — *Ribautiella amazonica* Scheller (Scolopendrellidae): Distribution of developmental stages in the soil at Lago Janauarí. Monthly samples taken every 3.5 cm to a depth of 14 cm between August, 1987 and April, 1988 (non-inundation period); total catch = 100%.

FIG. 3. — *Ribautiella amazonica* Scheller (Scolopendrellidae): Percentage of developmental stages caught in the soil (0-14 cm depth). Monthly samples taken between August, 1987 and April, 1988 (non-inundation period) at Lago Janauarí.

FIG. 4. — *Ribautiella amazonica* Scheller (Scolopendrellidae): Temporal occurrence and abundance of developmental stages (ind./m2) in the soil (0-14 cm depth). Monthly samples taken between August, 1987 and April, 1988 (non-inundation period) at Lago Janauarí.

FIG. 5. — *Ribautiella amazonica* Scheller (Scolopendrellidae): Temporal occurrence and abundance (ind./m2) of specimens in the soil at Lago Janauarí. Monthly samples taken every 3.5 cm to a depth of 14 cm between August, 1987 and April, 1988 (non-inundation period).

About 64% of the *Ribautiella* population in the seasonal mixedwater forest was represented by juveniles (Fig. 3), 12% by subadults and 24% by adults. The sex ratio of males and females was 1: 1.2 (n = 268). Population density was lowest two weeks prior to inundation (April 29, 1988: 250 ind. m-2), when most of the symphylans must have entered tree roots to pass flooding in a dormant state. Abundance was highest eight weeks after inundation had ended (September 30, 1987: 1,477 ind. m-2), due to a high number of juveniles of the progeny in the upper 7 cm of the soil (Figs 4, 5).

There was no clear correlation between the vertical distribution of *R. amazonica* in the soil throughout the non-inundation period and the abiotic factors monitored in the study area.

Source : MNHN, Paris

Symphylella adisi Scheller (Scolopendrellidae)

This is the smallest of the three species collected in the seasonal mixedwater inundation forest reaching a maximum of 1.5 mm in length. It was only found in the soil but was recorded from all soil layers sampled (Figs 6, 9). About 68% of its population was represented by juveniles, 11% by subadults and 21% by adults (Fig. 7). The sex ratio of males and females was 1: 1.1 (n = 35). The population density was lowest two weeks prior to forest inundation (April 29, 1988: 5 ind. m-2) and highest during the early rainy season (February 2, 1988: 327 ind. m-2). There was no correlation found between the population density of *S. adisi* and weather conditions in the area (dry season versus rainy season).

FIG. 6. — *Symphylella adisi* Scheller (Scolopendrellidae): Distribution of developmental stages in the soil at Lago Janauarí. Monthly samples taken every 3.5 cm to a depth of 14 cm between August, 1987 and April, 1988 (non-inundation period); total catch = 100%.

FIG. 7. —*Symphylella adisi* Scheller (Scolopendrellidae): Percentage of developmental stages caught in the soil (0-14 cm depth). Monthly samples taken between August, 1987 and April, 1988 (non-inundation period) at Lago Janauarí.

FIG. 8. — *Symphylella adisi* Scheller (Scolopendrellidae): Temporal occurrence and abundance of developmental stages (ind./m2) in the soil (0-14 cm depth). Monthly samples taken between August, 1987 and April, 1988 (non-inundation period) at Lago Janauarí.

FIG. 9. — *Symphylella adisi* Scheller (Scolopendrellidae): Temporal occurrence and abundance (ind./m2) of specimens in the soil at Lago Janauarí. Monthly samples taken every 3.5 cm to a depth of 14 cm between August, 1987 and April, 1988 (non-inundation period).

It is presumed, that *S. adisi* passed forest inundation in a dormant state in the soil. Due to its low abundance, it has not yet been located in soil samples taken under water during the flood period and the type of its retreat (naturally available or self-made) is still unknown. Six weeks after the forest floor had dried, adults and early juvenile stages of their offspring (8 and 9 pairs

Source : MNHN, Paris

of legs) were found in 3.5 - 14 cm soil depth (Figs 8, 9). Subadults occurred from end of October onwards. The highest number of juvenile stages was observed during the early rainy season (in February; Fig. 8) and main reproduction is assumed to occur at this time. The abundance of subadults subsequently declined and advanced juvenile stages (9 and 10 pairs of legs) as well as subadults dominated (Fig. 8). Ten weeks prior to inundation, only a few specimens were found and those solely in the lowest of the soil layers sampled (10.5 - 14 cm; Fig. 9). The main part of the population most probably had entered retreats at this time and, due to the dormant state, could not be obtained by means of the soil extraction method.

Based on the characteristics outlined, *S. adisi* is considered a terricolous non-migrating and univoltine species with dormant stages (presumably of subadults and advanced juveniles) in retreats under water during annual inundation.

Hanseniella arborea Scheller (Scutigerellidae)

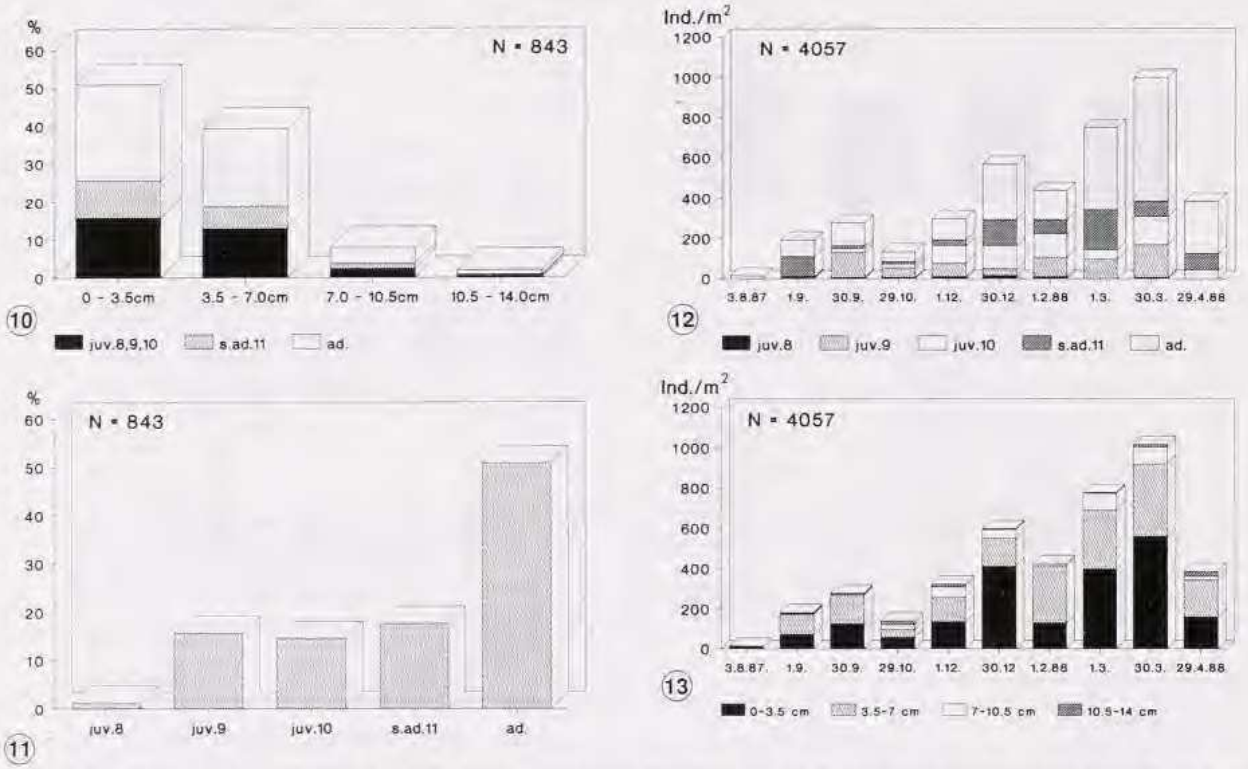

FIG. 10. — *Hanseniella arborea* Scheller (Scutigerellidae): Distribution of developmental stages in the soil at Lago Janauarí. Monthly samples taken every 3.5 cm to a depth of 14 cm between August, 1987 and April, 1988 (non-inundation period); total catch = 100%.

FIG. 11. — *Hanseniella arborea* Scheller (Scutigerellidae): Percentage of developmental stages caught in the soil (0-14 cm depth). Monthly samples taken between August, 1987 and April, 1988 (non-inundation period) at Lago Janauarí.

FIG. 12. — *Hanseniella arborea* Scheller (Scutigerellidae): Temporal occurrence and abundance of developmental stages (ind./m²) in the soil (0-14 cm depth). Monthly samples taken between August, 1987 and April, 1988 (non-inundation period) at Lago Janauarí.

FIG. 13. — *Hanseniella arborea* Scheller (Scutigerellidae): Temporal occurrence and abundance (ind./m²) of specimens in the soil at Lago Janauarí. Monthly samples taken every 3.5 cm to a depth of 14 cm between August, 1987 and April, 1988 (non-inundation period).

This terricolous, migrating and univoltine species reaches 2.7 mm in length. Adults are known to pass inundation in the trunk/canopy area of seasonal blackwater inundation forests

Source : MNHN, Paris

(ADIS & SCHELLER, 1984). This behaviour was reconfirmed for *H. arborea* from the seasonal mixedwater inundation forest (Fig. 14).

In the soil, about 51% of the population caught during the non-inundation period was represented by adults (the migrating stage), 31% by juveniles and 18% by subadults. The sex ratio of males and females was 1 : 1.5 (n = 429). *H. arborea* is considered hemiedaphic, as 51% of all specimens extracted from soil samples in 1987/88 were found in the top 3.5 cm and 90% in 0-7 cm soil depth, irrespective of their developmental stage (Figs 10, 13). Data differs somewhat from results obtained in the seasonal blackwater forest, where *H. arborea* was most abundant in 3.5 - 7 cm soil depth (47% of the total catch), and where only 12% of all specimens were obtained from the top 3.5 cm (ADIS & SCHELLER, 1984). First analysis of grain size and mineral composition of soils from mixed- and blackwater inundation forests (ADIS & IRION, unpubl.) indicated, that a lower abundance of *H. arborea* in the soil layers sampled corresponded with a greater presence of grains < 2 µm, due to a higher amount of clay. In the seasonal mixedwater forest under study, decrease in population density of *H. arborea* from the top 3.5 cm to 14 cm soil depth (cf. Fig. 10) was correlated with an increase of grains < 2 µm and of clay from 32% to 49% per soil layer ($p < 0.10$ for the total catch, $p < 0.05$ for monthly catches of Oct.10 and Dec. 12, 1987 & March 1 and 30, 1988). In the seasonal blackwater inundation forest, abundance of *H. arborea* was highest where the amount of grains < 2 µm and of clay was the lowest (12% in 3.5 - 7 cm soil depth) as compared to the soil layers below (25 - 31% in 7-14 cm depth), where abundance was lower (cf. Fig. 3 *in* ADIS & SCHELLER, 1984).

It is suggested, that *H. arborea* might have difficulties inhabiting fine and clayey soil layers due to its relatively large size.

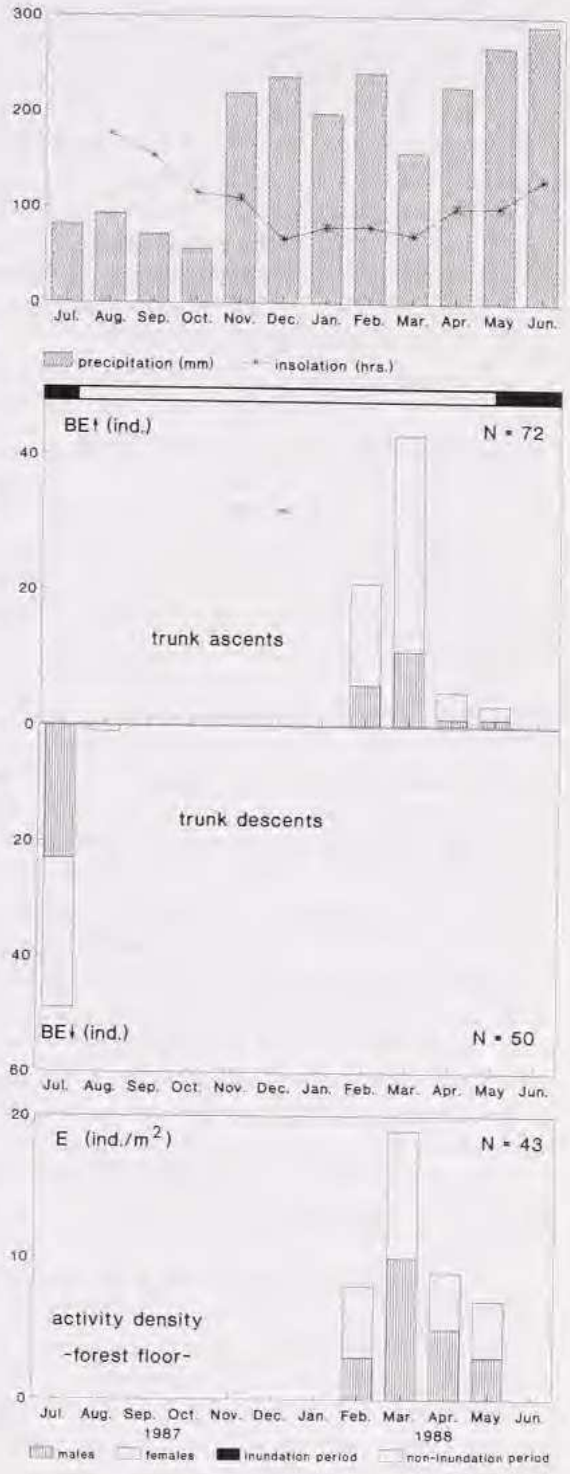

FIG. 14. — *Hanseniella arborea* Scheller (Scutigerellidae): Activity density of males and females on the forest floor (4 ground photo-eclectors: (E); ind./m²), trunk descents (BE ↓) and trunk ascents (BE ↑); one arboreal photo-eclector, respectively) between July, 1987 and June, 1988 at Lago Janauarí.

Source : MNHN, Paris

The lowest abundance of this species in soils from the mixedwater area was observed during the beginning of the non-inundation period (August 3, 1987: 14 ind. m^{-2}). *H. arborea* was at this time represented by adults which had returned from the trunk/canopy area after flooding and recolonized the upper 3.5 cm of the forest floor (Figs 12-14). Juvenile stages and subadults of the progeny were detected only four weeks later (Fig. 12). Their abundance was highest during the beginning of the rainy season (in December/January), shortly after the main reproduction must have occurred. Adults dominated between February and April (Fig. 12) when they came to the surface (where they were caught in ground photo-eclectors) and started ascending tree trunks, about 12 weeks prior to forest inundation (Fig. 14). The predominance of females assured the continuation of this species. During periods of less insolation, the number of adults caught in arboreal photo-eclectors was lower ($p < 0.05$). No significant correlation was found between catch numbers and the increasing water-level of the Rio Negro (cf. ADIS *et al.*, this volume). In the seasonal blackwater inundation forest, adults of *H. arborea* occurred more frequently in ground photo-eclectors after heavy rainfalls, compared to drier periods ($p < 0.05$; cf. ADIS & SCHELLER, 1984).

Phenology data of *H. arborea* from this mixedwater study area supports the life cycle proposed for this species based on results obtained by ADIS & SCHELLER (1984) from the seasonal blackwater inundation forest.

CONCLUSIONS

Four terricolous species of Symphyla were found to inhabit the soils of different non-flooded upland forests in Central Amazonia: *Scolopendrellopsis tropicus*, *Symphylella adisi*, *Ribautiella amazonica* (Scolopendrellidae), and *Hanseniella arborea* (Scutigerellidae; cf. SCHELLER, 1992).

Results of this paper show, that three of them succeeded in colonizing seasonally inundated forests of the mixedwater and blackwater type in the Rio Negro valley. The survival strategies which have evolved include a migratory state, represented by adults which pass inundation in the trunk/canopy area (Scutigerellidae) and a dormant state, represented by advanced juvenile and subadult stages which pass the flood period under water in retreats (Scolopendrellidae). The concentration of dissolved oxygen in the water body near the soil is known to be so low that flood resistant symphylans may have to switch from plastron and cutaneous respiration to anaerobic respiration (ADIS & MESSNER, 1991; MESSNER & ADIS, 1988, 1992). The first and second larval stages (6 and 7 pairs of legs respectively) of the three symphylan species may be inactive (TIEGS, 1945) or may only last a short time, as they were not obtained by means of the soil extraction method. Only the migrating species *H. arborea* was observed to respond to abiotic changes in its environment. Activity density on the soil surface and vertical migration were somewhat triggered by these secondary ecofactors which are no longer directly related to the cycle of flooding, and to which many terrestrial invertebrates of inundation forests have become sensitive (cf. ADIS, 1992a). The flood pulse (JUNK *et al.*, 1989) is regarded as the original determinant of trunk ascents and descents. However, it was found to act as the primary control mechanism or ecofactor among a few invertebrate species only (ADIS, 1992a).

Evaluation of capture data also indicated, that the three symphylan species changed from a plurivoltine mode of life in upland forests (ADIS, MORAIS, RODRIGUES & SCHELLER, unpubl.) to an univoltine life cycle in inundation forests. This was also observed in Pseudoscorpiones and Meinertellidae (Archaeognatha) from the same study areas (ADIS *et al.*, 1988; ADIS & STURM, 1987). It remains to be investigated if the species of Symphyla in inundation forests already differ ecologically and phenologically, as well as genetically, to such a great degree from those in upland forests that they must be regarded as new species or subspecies (cf. WOLF & ADIS, 1992).

Source : MNHN, Paris

ACKNOWLEDGEMENTS

We are indebted to all our colleagues at the National Institute of Amazonian Research (INPA) in Manaus (Brazil) and at the Max-Planck-Institute for Limnology in Plön (Germany) who, in the field or laboratory, contributed to this study, especially Susanne HAMANN, Irmgard ADIS, Edilson DE ARAUJO SILVA and M. Sc. Elizabeth FRANKLIN. Dr. Helen READ (Bucks, United Kingdom) kindly corrected the English manuscript. This study was supported by a grant from the German Academic Exchange Service (DAAD) for the second author and from the Max-Planck-Society for the third author. We wish to acknowledge the valuable support received by PD Dr. W. J. JUNK, head of the Tropical Ecology Working Group at the Max-Planck-Institute for Limnology in Plön, Germany.

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